

REPLY

Issues in the Coordination of Human Brain Activity and Motor Behavior

Armin Fuchs, Viktor K. Jirsa, and J. A. Scott Kelso

Center for Complex Systems and Brain Sciences, Florida Atlantic University, Boca Raton, Florida 33431

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We are grateful to Sanes for his comments on our work, particularly for placing it in the broader context of current neurophysiological and neuroanatomical evidence. For the most part, his remarks are well made and well taken. Here we wish to provide some further perspective and elaboration on some of the issues he raises. These fall into three main categories: strategies of investigation into the relation between the dynamics of the brain and the dynamics of behavior, theoretical development of our neural field theory of cortical function, and analysis and computational methods for extracting key information from human neuroimaging data.

Sanes understands that modern neuroimaging studies come with a double-edged sword. While they may provide access to the activity of underlying neural structures for small-amplitude finger movements (as in Kelso *et al.*, 1998), they cannot easily be tailored for more complicated, everyday actions. Normal reaching movements, for example, cannot be carried out by a subject inside a magnet or with a large array of SQUIDs around the head for pretty obvious reasons. Movement artifacts alone would drown out the underlying brain signals. Yet the issue concerning which movements are appropriate to study may not revolve around single versus multijoint movements, *per se*. For us the issue is rather which experimental paradigms (or model systems) afford the best entry point for understanding brain–behavior relations. For example, the discovery and ongoing study of behavioral phase transitions and related phenomena have proved useful because they have allowed identification of the relevant behavioral and neural variables (on a given level of description) and their coordination dynamics (equations of motion that capture the stability and change of coordination states). Our work on sensorimotor coordination referred to by Sanes derives from earlier empirical and theoretical studies of interlimb (multijoint!) coordination (e.g., Kelso, 1984; Haken *et al.*, 1985). It turns out that the dynamics which hold for bimanual

and sensorimotor coordination also apply to interpersonal (Schmidt *et al.*, 1998) and visual–manipandum (Stins and Michaels, 1999) coordination. While the latter cases certainly present a challenge to brain theory, both the bimanual and the sensorimotor cases have already been derived from the (admittedly primitive) neural theory of cortical function (in addition to the theoretical work described in Fuchs *et al.*, this issue).

Although some caution should be exercised in generalizing principles of neural control across apparently different classes of movement, it is interesting to note the similarity, at the level of the end effector, between the velocity profiles of the finger movements studied by Kelso *et al.* (1998) and reproduced in the Fuchs *et al.* (this issue) theoretical model and the velocity profiles of multidegree of freedom upper limb movements first reported by Kelso *et al.* (1979; see also Harris and Wolpert, 1998). There is some reason, then (though as Sanes remarks, this needs experimental confirmation), to suppose that the same neural control principle applies to the end effector, regardless of whether the movements are single or multijoint or even those produced during speech (Kelso *et al.*, 1986).

Related is the issue of direction of movement. At the current level of analysis a flexion movement and an extension movement manifest themselves essentially in the same way in noninvasively recorded brain signals. We do not know yet where the directional coding comes in. Although there are some hints in the data more systematic studies on this topic are necessary.

Going beyond purely physical parameters of a limb movement such as amplitude and velocity and how they are represented in the brain signal we have the complex problem of how the brain interacts with its environment. Already the seemingly simple case of rhythmic finger movement paced by a metronome opens an entirely new class of phenomena on both the behavioral and the brain level. Just as an example, when a subject is instructed to perform a flexion movement between two beats of a metronome and the pac-

ing frequency is increased s/he switches spontaneously to a synchronized coordination pattern at a certain pacing rate. If, however, the subject intentionally starts by performing an extension movement on the beat (which is very similar to the former flexion off the beat) the coordination pattern is stable at much higher movement frequencies (Kelso *et al.*, 1990). This shows that much more is going on in the brain than simple coding of physical movement quantities. Again, some clues have been found in the MEG signal (e.g., Fuchs *et al.*, 1999; Kelso *et al.*, 1998); certainly further investigation is needed.

In terms of getting the finger to the right place at the right time, velocity appears to play an important role. If one examines the error in timing in relation to possible movement parameters, one finds the strongest correlation ($r = 0.99$) between the timing of the peak velocity and the synchronization error (Kelso and Cohn, unpublished observations). This makes sense: peak velocity reflects the onset of finger deceleration. Decelerate early and you arrive early; decelerate late and you arrive late. It doesn't have to be this way; for example, synchronization error could be correlated to the initial "preprogrammed" force, but this is not so. The same relation appears to hold between the brain signals and timing error, not surprising given the strong coupling between brain activity and movement velocity.

On the theoretical side the major difference of the neural field theory to other models of cortical function is the spatiotemporal scale of brain activity. Cortical network models typically evoke space and time scales of 0.1–10 mm and 1–10 ms. Here we aim at a description of large-scale brain activity detected by EEG and MEG. A model of such activity has to consider time delays via propagation along white matter tracts and a topographic organization of afferent and efferent peripheral fibers in the cortex. Both are established in the neural field theory (Jirsa and Haken, 1996), the latter by the notion of functional input and output units. However, the anatomical and functional internal organization of the cortical network is not considered as pointed out by Sanes. On the local level, i.e., intracortically, this simplification can be justified by space and time scale considerations resulting in averaging. On the global level involving interareal connections, however, the internal organization should not be neglected. Thus the assumption of a spatially invariant fall-off of connectivity is an oversimplification. Here the only justification is pragmatic, namely the initial study of an oversimplified system followed by progress to a more realistic situation by incorporating interareal fiber tracts into the connectivity matrix of the neural field theory. An additional time dependence of these matrix elements realized by a learning dynamics introduces plasticity. Recently we developed a paradigmatic

model system to study the effects of interareal connections and plasticity (see Jirsa *et al.*, 1999): A fiber tract connects symmetrically two areas A and B in a continuous cortical sheet with local connections. At a threshold value of synaptic weights of the connection A–B the neural activity of the entire sheet becomes unstable, synchronizes, and performs spatiotemporal pattern formation. By varying the location of one of the terminals, say B, the pattern formation process can be controlled and the neural activity can be guided systematically through a series of spatiotemporal bifurcations or phase transitions.

We are pleased to learn from Sanes about recent evidence (Sanes and Donoghue, 2000) regarding the distributed, overlapping representations of fingers, wrist, elbow, and shoulder in motor cortex. This fits behavioral data and theory that voluntary control of multidegree of freedom movements is through synergies or coordinative structures, self-organized groupings of neurons, muscles, and joints that are constrained to act as a single functional unit. Some of these constraints have been identified (e.g., relative timing among participating muscles and joints, straight line trajectories, bell-shaped velocity profiles) and are the subject of intensive current research on motor control. Here again, in line with the tenor of Sanes' remarks, it will be important to directly connect identifiable behavioral and task constraints to the functional organization of the motor cortex and other relevant regions.

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